

# Diversity and Biogeography of Subterranean Guano Arthropod Communities of the Flinders Ranges, South Australia.

TIMOTHY MOULDS

Centre for Evolutionary Biology and Biodiversity, School of Earth and Environmental Sciences, The University of Adelaide, South Australia 5005.  
timothy.moulds@adelaide.edu.au

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This study documents the arthropod diversity and ecology of guano-associated species in 12 caves and mines of the Flinders Ranges, South Australia. Twenty two species from 12 orders and two classes are recorded. This represents a five-fold increase in species richness across the region from previously published and unpublished records. Eregunda Mine and Weetootla Gorge Mine 2 were the most diverse with five and six species recorded respectively. Specious groups included the tenebrionid beetle genus *Brises* and the emesine reduviid bug genus *Armstrongula*. Guano communities in the Flinders Ranges contain species in common with the Nullarbor Plain to the west and isolated arid karst areas to the north. There are few affinities with species found in the moist coastal regions of south-eastern Australia.

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## INTRODUCTION

Guano-associated invertebrate communities are poorly known for the vast majority of Australian caves. Animals in these communities are classified according to their ecological dependence on guano as either obligate guano-dwelling animals (guanobites), opportunistic guano-dwelling animals (guanophiles) or transitory guano-dwelling animals (guanoxenes) (Gnaspini and Trajano 2000; Humphreys 2000). The composition and evolution of guanophilic arthropod communities is dramatically different from resource-poor troglobitic (obligate cave-dwelling) communities (Gnaspini 1992; Gnaspini and Trajano 2000). The presence of virtually unlimited food resources enables a wide diversity of normally epigeal (surface-dwelling) species to utilise the stable conditions found in caves. This has been previously demonstrated by studies in the south-east and Nullarbor Plain karst areas of South Australia (Richards 1971; Moulds 2004).

Several karst regions containing guano deposits are located in South Australia, ranging from high rainfall coastal areas such as Kangaroo Island and the lower south-east, to dry arid areas such as the Nullarbor Plain, Flinders Ranges and Davenport

Ranges. The guanophilic arthropod assemblage in the maternal chamber of Bat Cave, Naracoorte, located in the upper south-east of South Australia, has received the most intensive study for guano invertebrates in Australia (Hamilton-Smith 2000; Sanderson 2001; Bellati et al. 2003; Moulds 2003). A major study of cavernicolous arthropod diversity and ecology on the Nullarbor Plain (Richards 1971) documented the subterranean communities, including those associated with guano. This was the first Australian study to document guanophilic arthropod ecology and provide possible geographic relationships with other Australian guanophilic communities.

The Flinders Ranges, situated between the immense karst area of the Nullarbor Plain to the west, and the karst areas of south-eastern South Australia, contain a number of widely-scattered caves in horizontal or gently dipping Neoproterozoic crystalline limestone (Lewis 1976; Webb et al. 2003). Many of these caves support small (< 50) transient populations of cave-dwelling bats, dominated by the inland cave bat (*Vespadelus findlaysoni* Kitchener, Jones and Caputi), with the chocolate wattled bat (*Chalinolobus morio* Gray) occasionally recorded. The only previously published accounts of guanophilic arthropods for the Flinders Ranges are records of the beetle *Brises acuticornis* Pascoe from three caves

(Hamilton-Smith 1967; Mathews 1986). In addition, several unpublished records of undetermined Acarina, Coleoptera (Carabidae) and Diptera (Nycteriibidae) were recorded by Elery Hamilton-Smith (Moulds 2004).

This study was undertaken due to the paucity of knowledge of cavernicolous invertebrates, specifically guano invertebrates, of this important biogeographic region that links the comparatively well-studied eastern and western karst regions of South Australia. The diversity of guano-associated arthropods in 12 exemplar caves and mines of the Flinders Ranges is documented. Data collected through direct observation and relevant literature are combined to summarise species interactions as a food web. Biogeographic relationships of guanophilic arthropods are believed to be more closely related to nearby arid karst areas

than to wetter coastal areas. These relationships are assessed and discussed.

METHODS

Nine caves and three mines were sampled during two field trips in April and September 2003 (Fig. 1). Specimens were primarily collected individually using hand-held forceps due to the extremely localised guano deposits at most sites (Upton 1991). Guano samples were also taken from Weetootla Gorge Mines, Eregunda Mine, and Chambers Gorge caves for extraction of arthropods in Tullgren funnels as described by Upton (1991). Guano was also collected when available in sufficient quantities and measured for pH, allowing micro-habitat conditions

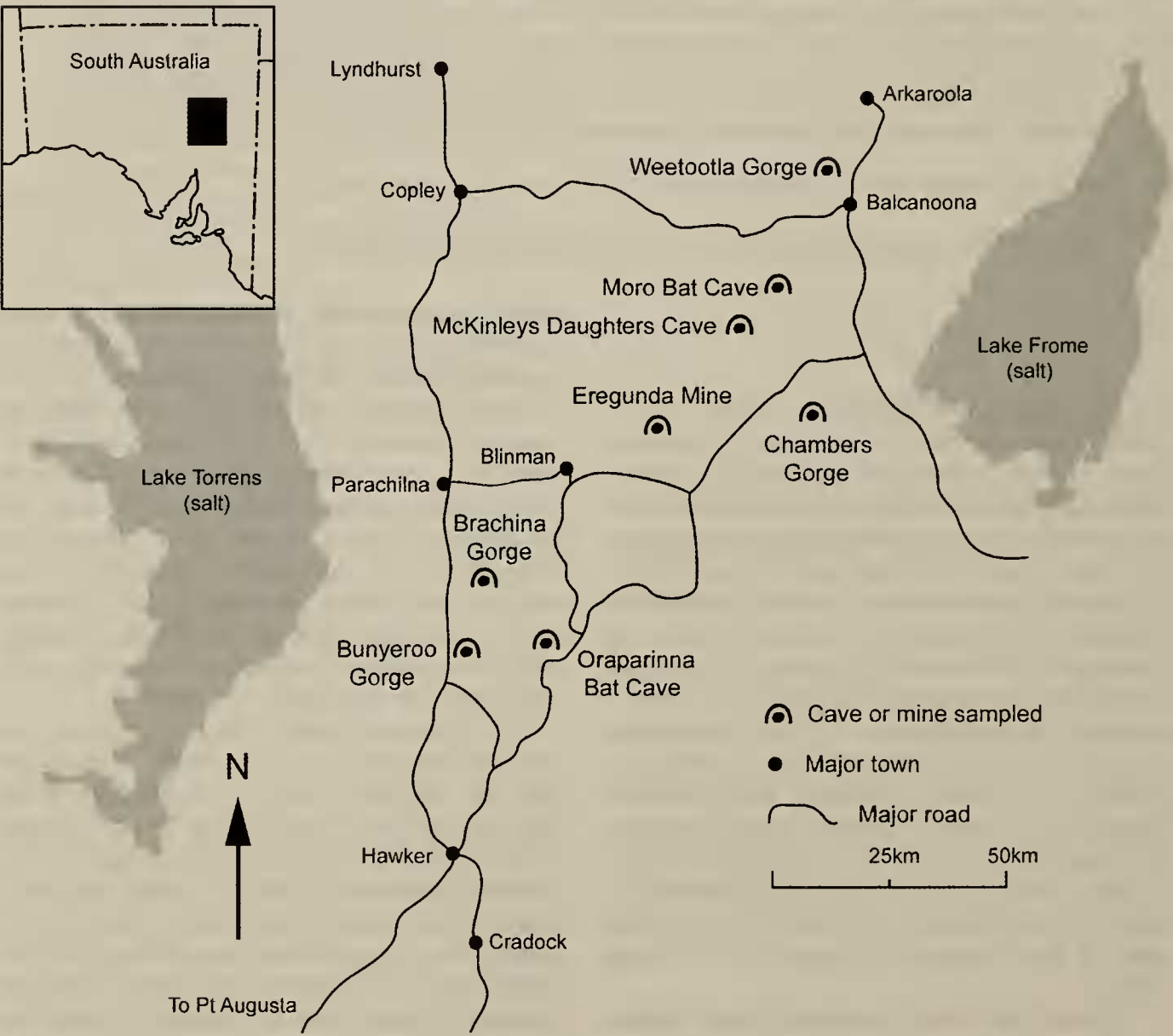


Figure 1. Localities of guano sites visited in the Flinders Ranges. Brachina, Bunyeroo, Chambers, and Weetootla gorges all contain two sites.



to be assessed. The caves examined during this study do not include every guano-bearing cave in the area, but rather represent a cross-section of active bat caves found throughout the Flinders Ranges. A list of all Flinders Ranges caves historically known to contain guano can be found in Hamilton-Smith et al. (1997).

### Terminology

Australian caves are referred to by a binomial alpha-numeric system according to Mathews (1985), with those of the Flinders Ranges using the prefix 'F'. Mines are not included in this system and are referred to by name only. The division of caves into four environmental zones (entrance, twilight, transition, and deep zones, according to the amount of light and degree of interaction with surface climatic conditions) follows Humphreys (2000).

### Cave and mine site descriptions

The majority of caves examined during this study are small, rarely extending into complete darkness or attaining a deep zone. Weetootla Gorge in the Gammon Ranges was the northern-most area examined. Weetootla Gorge Mines 1 and 2 (Fig. 1) are horizontal magnesite adits excavated prior to the early 1970s. The entrances were gated in the early 1990s with 15 cm grids preventing access by large animals, although inland cave bats are still able to negotiate the entrances. Weetootla Gorge Mine 2 was found to contain 36 inland cave bats, counted using an infrared video of the flyout at dusk (T. Reardon, pers. comm. 2003). The adit is approximately 90 m long and breaks into a natural rift at its termination. Bat roosts are located near the end of the adit, 50–70 m from the entrance. Small guano piles 1 m wide by 1–2 m in length lie directly on the solid magnesite floor. Weetootla Gorge Mine 1, located 200 m downstream of Weetootla Gorge Mine 2, contained only two widely separated guano piles with no evidence of fresh guano. No bats were sighted inside this adit, suggesting the roost is used infrequently.

The remainder of mines and caves examined were situated in the northern and central Flinders Ranges and are described from north to south (Fig. 1). Moro Bat Cave (F47), located in Moro Gorge, is 50 m above a permanent stream and extends into the cliff face terminating in the transition zone. The cave contains several bat guano deposits and dung of the yellow-footed rock wallaby (*Petrogale xanthopus* Gray) which uses the entrance area as a daytime retreat. The vertical slot entrance to McKinleys Daughters Cave (F175) located near stream level leads to a narrow high aven (terminal roof hole). A thin veneer of dry guano and numerous small mammal bones sit on a fine

silt floor in the twilight zone. Unidentified bats were present high in the aven. Eregunda Mine, north-east of Blinman, is a 25 m long adit containing several guano deposits under an active roost of inland cave bats (for further details see Moulds, in press). Two unnamed caves, on the southern side of Chambers Gorge in a high valley, contain several inland cave bats and substantial desiccated guano in the transition zone chambers. Two caves near the Teamster's Campsite in Brachina Gorge contain minor guano deposits mixed with fine soil. One of these is located at river level and the other approximately 40 m above the river. Two caves at the western end of Bunyeroo Gorge, near river level, are small with only one reaching the transition zone and the other only containing a twilight zone. Oraparinna Bat Cave, located north of Wilpena Pound, contained extensive amounts of guano within the primarily horizontal joint controlled passages.

### Guano microhabitat conditions

Guano caves in the Flinders Ranges often have extremely low relative humidities and are commonly characterised by dry, acidic, pellet-like guano, even under active bat roosting areas that normally have moist, basic conditions (Harris 1970; Decu 1986; Gnaspini and Trajano 2000). Weetootla Gorge Mines 1 and 2 had relative humidities less than 20% during September 2003. This has consequently affected the water content of guano deposits, which have been historically recorded from 3.3% (Arcoota Creek Cave) to 12.7% (Clara St. Dora Cave) (Winton 1922), comparable to the driest guano found in Bat Cave, Naracoorte (Moulds 2003). Several artificial entrances in Oraparinna Bat Cave opened for guano mining have been the cause of desiccated guano piles near these entrances, limiting the distribution of some arthropods. Despite an active bat roost in Weetootla Gorge Mine 2, virtually no fresh guano was found. The guano beneath an active bat roost in Weetootla Gorge Mine 2 had a pH of 5.5.

## RESULTS

### Species recorded

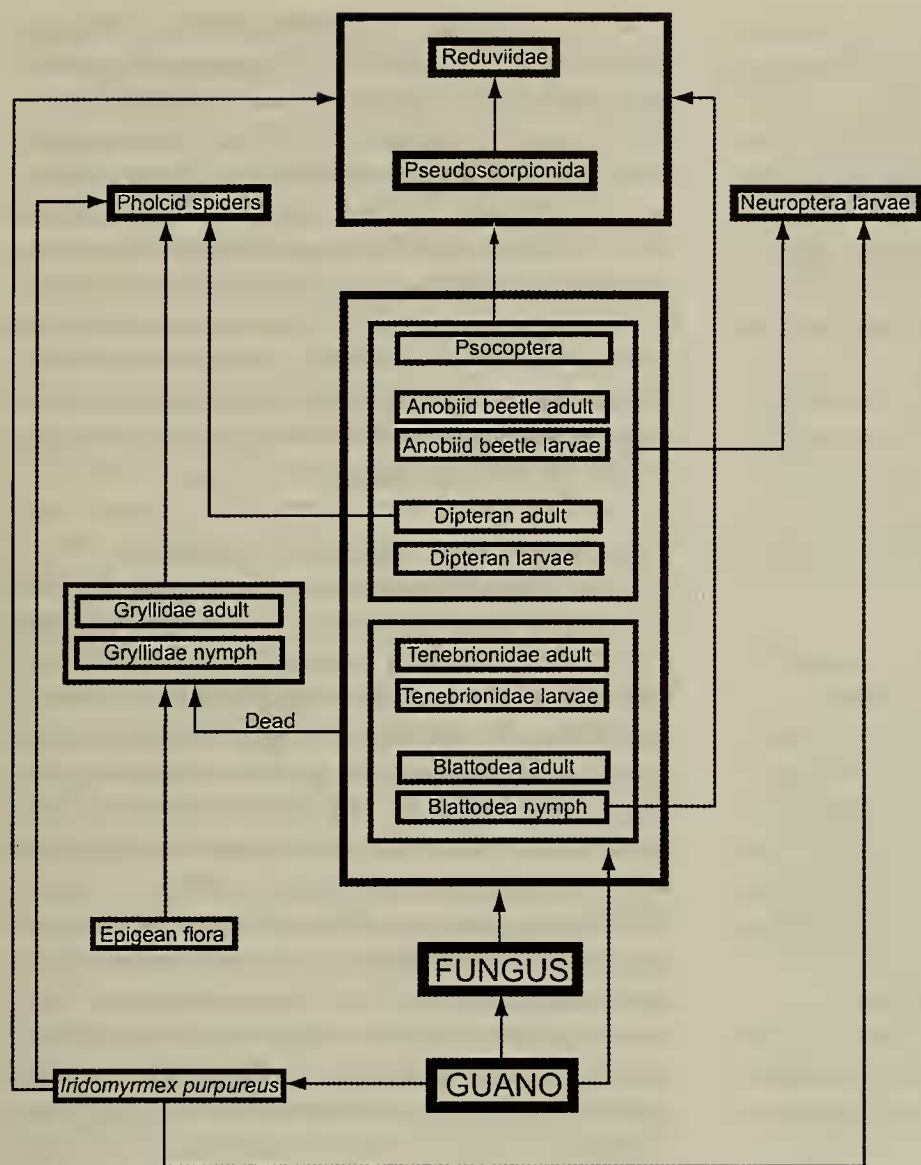
Twenty two arthropod species were collected from 12 orders and two classes (Table 1). This represents a substantial increase from the single species previously recorded in the literature (*Brises acuticornis*) and the four unpublished species records of Elery Hamilton-Smith. Two sites, Eregunda Mine and Weetootla Gorge Mine 2, were extremely diverse with five and six orders recorded respectively. Active arthropod communities were found at all 12 sites, but not in

SUBTERRANEAN GUANO ARTHROPODS

Location	Cave	Order	Family	Genus	Species
Brachina	Unnamed	Coleoptera	Anobiidae		sp 1
Gorge	river cave	Neuroptera	Myrmeleontidae	<i>Aeropteryx</i>	sp 1
	Unnamed hillside cave	Neuroptera	Myrmeleontidae	<i>Aeropteryx</i>	sp 1
Bunyeroo Gorge	Unnamed cave no.1	Hemiptera	Reduviidae	<i>Armstrongula</i>	sp 1
	Unnamed cave no.2	Hemiptera	Reduviidae	<i>Armstrongula</i>	sp 2
Chambers Gorge	Unmaned cave no.1	Neuroptera	Myrmeleontidae	<i>Aeropteryx</i>	sp 1
		Zygentoma	Nicoletiidae	<i>Trinemura</i>	sp 1
	Unnamed	Araneae			sp 1
	bat cave	Neuroptera	Myrmeleontidae	<i>Aeropteryx</i>	sp 1
		Orthoptera	Gryllidae		sp 1
Mount McKinley	McKinleys Daughters Cave (F175)	Diptera			sp 1
		Hemiptera	Reduviidae	<i>Armstrongula</i>	sp 1
		Neuroptera	Myrmeleontidae	<i>Aeropteryx</i>	sp 1
Moro Gorge	Moro Bat Cave (F47)	Lepidoptera	Noctuidae	<i>Dasypodia</i>	<i>selenophora</i>
		Lepidoptera	Pyalidae		sp 1
		Neuroptera	Myrmeleontidae	<i>Aeropteryx</i>	sp 1
Oraparinna	Oraparinna Bat Cave (F8)	Coleoptera	Anobiidae	<i>Ptinus</i>	<i>exulans?</i>
		Coleoptera	Anobiidae		sp 1
		Coleoptera	Tenebrionidae	<i>Brises</i>	<i>acuticornis</i>
Point Well	Eregunda Mine	Araneae	Pholcidae		sp 1
		Coleoptera	Tenebrionidae	<i>Brises</i>	undetermined
		Hymenoptera	Formicidae	<i>Iridomyrmex</i>	<i>purpureus</i>
		Pseudo-scorpionida	Cheliferidae	<i>Protochelifer</i>	sp 1
		Psocoptera			sp 1
Weetootla Gorge	Mine 1	Araneae	Pholcidae		sp 2
		Coleoptera	?Dermestidae		sp 1
	Mine 2	Araneae	Pholcidae		sp 3
		Blattodea			sp 1
		Coleoptera	Tenebrionidae	<i>Brises</i>	<i>caraboides</i>
		Hemiptera	Reduviidae	<i>Armstrongula</i>	sp 3
		Neuroptera	Myrmeleontidae	<i>Aeropteryx</i>	sp 1
		Orthoptera	Gryllidae		sp 1

Table 1. Arthropods collected from guano deposits in the caves and mines of the Flinders Ranges. Caves are listed alphabetically by the area in which they are found. Some specimens could only be identified to subfamily or genus.





**Figure 2. Food web of a Flinders Ranges guano community. Arrows represent the direction of energy flow within the food web. Guano ecosystems are extremely variable, consisting of numerous micro-habitats differentiated by moisture, pH and temperature. Fungi and bacteria are an important basis for guano ecosystems, providing usable nutrients for many species unable to consume guano directly.**

very old guano deposits that were extremely dry and powdered. The beetle *B. acuticornis duboulayi* Bates (Tenebrionidae) was found in Oraparinna Bat Cave and an unidentified *Brises* larvae in Eregunda Mine. The second record of *B. caraboides*, from Weetootla Gorge Mine 2, greatly increases the distribution of this species, previously known only from the type locality near Eucla on the Nullarbor Plain. The emesine reduviid genus *Armstrongula* (Hemiptera) (Table 1) has a wide distribution in the Flinders Ranges, with three undescribed species recorded. Previously known species of *Armstrongula* are recorded from under bark near the Bogan River, New South Wales (Wygodzinsky 1950). The presence of an unidentified *Protochelifer* species (Pseudoscorpionida) in Eregunda Mine in

the central Flinders Ranges is an important intermediate record for this widespread, and often cavernicolous genus, between the Nullarbor Plain and the south-east of South Australia. The cosmopolitan beetle *Ptinus exulans* Erichson (Anobiidae), and an unidentified anobiid, were also recorded from Oraparinna Bat Cave.

### Food web and species interactions

A food web for the Flinders Ranges hypogean guano communities is shown in Figure 2. This was constructed using numerous direct field observations of many taxa combined with previously documented feeding biology of taxa from the literature.

The trophic basis of all the discrete ecosystems examined is bat guano. Tenebrionid beetle adult and larvae (*B. caraboides*) and nymphal cockroaches were observed directly scavenging on guano deposits in Weetootla Gorge Mine 2. Tenebrionid beetles also act as general scavengers of organic material. Meat ants (*Iridomyrmex purpureus* Smith) were observed in the twilight zone of Eregunda Mine removing fresh guano and carrying it to their nest, possibly as a food source (Moulds, in press). The presence of ants

adds a unique element to the species interactions at this locality by providing a potentially rich external food source for many of the predatory species such as pholcid spiders, reduviid bugs and neuropteran larvae. More commonly, guano deposits form a direct energy source for a succession of bacteria, yeast and fungi that support the majority of arthropods found in these environments (Fletcher 1975). Anobiid beetles have been recorded feeding on fungi and insect remains in guano deposits and spider webs (Richards 1971; Hickman 1974).

Gryllid crickets shelter in caves during the day and feed on plant material growing near cave entrances when conditions are favourable, similar to raphidopohorid cave crickets (Richards 1961, 1965,

1966). An individual was observed in September 2003 feeding upon arthropod remains in an unnamed bat cave in Chambers Gorge.

Myrmeleontid neuropteran larvae are common inhabitants of sandy floors in entrance and twilight zones, capturing small arthropods including ants, small beetles, fly larvae, and Psocoptera that fall into their conical pits. The presence of guano near neuropteran pits attracts additional prey for these sedentary predators, making guano deposits a beneficial habitat. In the larval stage, Neuroptera are part of guano food webs, but the adults play little role other than foraging for both plant and animal food in the epigeal environment (New 1991). Adult Neuroptera were, however, commonly found during the day, sheltering in many of the caves examined (Table 1).

Reduviid bugs of the subfamily Emesinae are common predators in many subterranean guano deposits, stalking arthropods in small groups (Moulds, unpublished data). Individuals were observed in September 2003 on the guano surface in McKinleys Daughters Cave and caves in Bunyerroo Gorge. These bugs form the top predator within the Flinders Ranges guano deposits. Prey were generally consumed where captured, although sometimes were dragged away from guano deposits for later consumption.

A single cheliferid pseudoscorpion individual was also found in guano deposits. Pseudoscorpions spend most of the time under rocks, only emerging to hunt micro-arthropods.

## DISCUSSION

### Environmental limitations of population size

The most limiting factors against the development of large guanophilic arthropod communities in the Flinders Ranges are low humidity and transient bat populations that limit guano sites in volume and continuity. Guanophilic communities commonly inhabit environments of saturated humidity with many species preferring the strongly basic conditions associated with fresh guano (Moulds 2003). Low humidity, common in the Flinders Ranges, severely reduce fungal growth as many of the opportunistic phycomycetes found on fresh guano are susceptible to desiccation (Poulson 1992; Poulson and Lavoie 2000). Reduced growth of fungi, the primary food source of guanophilic communities, results in lower species abundance and diversity when compared with guanophilic communities in more humid locations such as coastal south-eastern Australia (Yen and Milledge 1990; Eberhard and Spate 1995; Bellati

et al. 2003). Further, the paucity of moist substrates removes key refugia for the numerous moisture-dependant species commonly found in guano caves. Consequently, families such as Jacobsonidae, Sciaridae and Sphaeroceridae are notably absent from the Flinders Ranges, and have been replaced by arid-adapted species such as tenebrionid beetles. Arid-adapted species comprise a substantial part of the species richness for caves across the entire region. The often stochastic semi-permanent bat colonies in the Flinders Ranges can have catastrophic consequences for guanophilic arthropod communities reliant on fresh moist guano for survival.

### Biogeography and dispersal mechanisms

The guanophilic arthropod fauna of the Flinders Ranges shows closest similarity in species diversity to that of the Nullarbor Plain and isolated karst areas to the north and east. The tenebrionid beetles *Brises acuticornis*, *B. caraboides* and the carabid *Thenarotes speluncarius* Moore are found in both regions (Moore 1967; Richards 1971; Mathews 1986). *Brises acuticornis* is recorded from epigeal and hypogeal habitats and may use rabbit or wombat burrows for shelter during the day, aiding in long range dispersal ability (Mathews 1986). The major extension to the known distribution of *B. caraboides* from near Eucla on the Nullarbor Plain to the Gammon Ranges in the northern Flinders Ranges is significant as it provides additional species similarities between these two regions.

The isolation of three species of *Armstrongula* within the Flinders Ranges suggests that increasing aridity through the region may have prevented the movement of hydrophilic cavernicolous species between karst areas. The disjunct karst formations of the region are also likely to have restricted the dispersal ability of other species. The occurrence and distribution of emesine reduviid bugs in guano caves, including those of the Flinders Ranges, is presently poorly understood but no records are known for this subfamily from the wetter southern karst areas of Australia.

The relationship of the single *Protochelifer* (Pseudoscorpionida) collected from the Flinders Ranges (Eregunda Mine) to *P. naracoortensis* Beier from south-east South Australia and to *P. cavernarum* Beier from the Nullarbor Plain is unknown at present. It is unclear if this single record from the Flinders Ranges is indicative of a paucity of pseudoscorpions in general or simply a result of minimal collecting.

The guano mite *Uroobovella coprophila* Womersley, ubiquitous in southern Australian bat caves, is notably absent from the Flinders Ranges and



other arid localities (Moulds 2004). This is probably due to rapid desiccation of fresh guano, even beneath active bat roosts, excluding this mite as it relies upon fresh, moist, highly basic guano and virtually disappears during periods when these conditions are not available (Harris 1973). This species shows a strong association with breeding colonies of the large bent-wing bat, *Miniopterus schreibersii* (Kuhl), which does not occur in the Flinders Ranges or other arid regions (Churchill 1998). The similar distribution pattern of *U. coprophila* and *M. schreibersii* suggest this mite may be phoretic on bats or guano-associated invertebrates such as carabid beetles, although no observations have been reported. Phoresy requires further investigation to determine its importance in the distribution of this, and other, guano-associated species.

The change in fauna composition moving south from the Flinders Ranges into the wetter coastal areas of south-eastern Australia is marked, with several taxa such as the guano mite *U. coprophila*, histerid beetles and phorid flies becoming dominant on fresh guano. This study represents only a first step in documenting the diversity of cavernicolous guanophilic arthropods in the Flinders Ranges. Many previously known caves remain to be investigated and new caves are still being discovered. The transient nature of bat colonies and their relatively small numbers make the study of guanophilic fauna difficult. However, the region warrants further attention as it represents an important interface between the cavernicolous fauna of the Nullarbor Plain and the wetter coastal areas of south-eastern Australia.

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